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SEASONAL ABUNDANCE OF MILLIPEDES IN A MEDITERRANEAN OAK FOREST (SOUTHERN FRANCE)

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ABSTRACT

The millipede community of a holm oak forest (*Quercus ilex*) in southern France was sampled seasonally for 2 yr, at two depths in the forest floor. Despite the strong seasonality of climatic conditions, both recruitment periods and vertical displacements in the soil change markedly according to species; contrasting examples are provided by *Glomeris marginata*, which breeds in summer and burrows in winter, and by *Opisthocheiron elegans*, which behaves the opposite way. At the community level, biomass changes significantly between a spring minimum and an autumn maximum. Such a pattern results from the high abundance of *G. marginata* , a drought-resisting species which grows and reproduces during summer but experiences substantial winter mortality. The seasonal pattern is different in number of individuals due to the minute litter-dweller *Polyxenus lagurus*, which has a low population density in early autumn. The biomass of macrosaprophagous millipedes on the site (annual mean of 10.5 g live weight m^{-2}; autumn peak of 14.6 g live weight m^{-2}) is much higher than that recorded further north in Europe, and its significance for litter consumption in Mediterranean forest is discussed.

INTRODUCTION

There is little quantitative data on the composition of communities of millipedes (Diplopoda) in Mediterranean ecosystems. The bulk of knowledge on the abundance of soil invertebrates concerns mesofauna (cf. Di Castri and Vitali-Di Castri, 1981), and millipedes, when mentioned, are usually considered at the supra-ordinal taxonomic level (Chilognatha vs. Penicillata). An essential aspect in assessing the effects of these animals in decomposition processes — the biomass of different trophic groups and its seasonal variation — has seldom been investigated, except for some results from the European part of the Mediterranean Basin. Saulnier and Athias-Binche (1986) and Karamaouna (1987) recorded low biomass figures in southern France and southern Greece, respectively. On the other hand, Janati-Idrissi (1988) showed that the biomass of macrosaprophagous populations could be very high in soils on limestone near

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Montpellier (France), whether in a *Quercus ilex* forest (Puechabon) or a *Quercus coccifera* garrigue (Saint Gely).

A more detailed study on the millipede community of the forest of Puechabon has been carried out for two years and, in this paper, its species composition is fully described both in terms of individuals and in biomass. Owing to the strong seasonality of the Mediterranean climatic conditions in the upper soil layers (Lossaint and Rapp, 1978; Iatrou and Stamou, 1989), particular attention has been paid to seasonal changes in abundance within the community. Assuming that there is no mass migration between sites, seasonal changes in abundance can be ascribed to recruitment and mortality, which has been examined for each species. However, an apparent decrease in density can also result from temporary burrowing of animals into the deep soil, below the sampling depth (Lamotte and Blandin, 1989). Accordingly, the seasonal changes in the vertical distribution of species have been taken into account to get an insight into the community dynamics.

METHODS

STUDY SITE

The study site is located in the state forest of Puechabon, Herault, 25 km northwest of Montpellier (3°35' 52" E; 43°44' 28" N), at an altitude of 260 m. The climate, though rather humid with a cool winter, is typically Mediterranean. Rainfall is minimal in summer with a period of severe drought almost every year; the summer dryness index of Emberger (1943) is <7. Overall, the weather conditions during the present study conformed to the normal pattern (Fig. 1).

A red fersiallitic soil, more brown in the upper layers, overlies karstic limestone; its clay content is high, as is the proportion of stones. The humus form is a mull, and measurements from nearby sites have given pH ≈ 7 and C/N ≈ 16 (Floret et al., 1989; Merzouki et al., 1989).

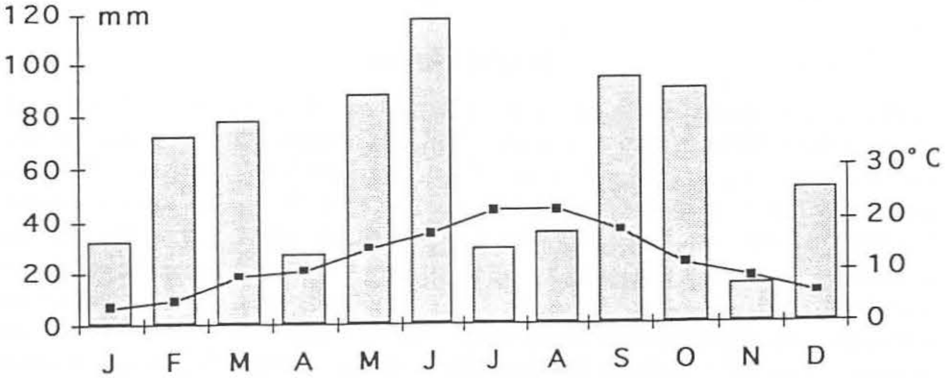

Fig. 1. Monthly mean temperature of the air (line) and mean rainfall (bars) at Puechabon for the two years of study (1991 and 1992), showing the typical summer dryness in July and August.

The forest is a holm oak coppice (*Q. ilex*) with a typical heterogeneous understorey of shrubs and herbs made up of several tens of species (Braun-Blanquet, 1936). The dense coppice, characterized by *Ruscus aculeatus*, *Hedera helix*, and *Buxus sempervirens*, is interspersed with open areas characterized by *Thymus vulgaris*, *Brachypodium ramosum* and *Juniperus oxycedrus*.

SAMPLING

Sampling was carried out in an area of about 3000 m^2 surrounding a cleared plot with a CNRS meteorological station. Eight samples, each including between 10 and 12 sampling units, were taken over two years: two in spring (30 April 1991 and 1 May 1992), two in early summer (5 June 1991 and 23 June 1992), two in early autumn (7 October 1991 and 1 October 1992), and two in winter (3 January 1992 and 29 January 1993). Each sampling unit consisted of two parts: (i) litter and soil down to about 2 cm deep, collected in a 25 × 25 cm quadrat (1/16 m^2); (ii) soil between 2 and 10 cm deep, collected with a cylindrical corer 10 cm in diameter ($\approx$ 1/127 m^2). More accurate stratification was impossible due to stones. The largest millipedes were sorted by hand in the laboratory, and the others extracted by Tullgren funnels 25 cm in diameter. Species were determined according to Demange (1981).

In order to assess the fresh biomass of Chilognatha, as many individuals as possible were weighed alive after cleaning on moist filter paper, then their species, sex, and stadium were determined. For dead animals, the mean live weight corresponding to their species, sex, and stadium was used. The biomass of Penicillata, represented by the minute *Polyxenus lagurus*, was not measured.

Population densities were expressed as both numbers of individuals and fresh biomass per unit area (m^2). Stadium I individuals of *P. lagurus* and *Polyzonium germanicum* were not taken into account, for the tiny, not very mobile stages are clumped and therefore difficult to sample.

The differences in abundance between samples were compared by means of parametric (Student's *t*-test) and nonparametric (Mann–Whitney U-test) methods (Sokal and Rohlf, 1981). The differences were considered significant if both tests gave a probability < 0.05.

RESULTS

SEASONAL ABUNDANCE OF SPECIES

A total of seven species were found at Puechabon. Four were present in all the samples: *Glomeris marginata* (Villers), *Cylindroiulus caeruleocinctus* (Wood), *Polyzonium germanicum* Brandt, and *Polyxenus lagurus* Linné. Another, *Opisthocheiron elegans* Ribaut, was present in seven out of eight samples. Two other species were found occasionally on the site: one specimen of *Ommatoiulus rutilans* (C.L. Koch) was collected in the samples and several others by hand, which made it possible to determine an adult male; two specimens of *Polydesmus* sp. were collected by hand.

Table 1
Seasonal abundance of the principal millipede species at Puechabon. The results are in numbers and biomass m^{-2} ± standard error

		Spring (21 s.u.)	Early summer (22 s.u.)	Early autumn (22 s.u.)	Winter (24 s.u.)	Mean
G. marginata	Ind. m^{-2}	100 ± 16	216 ± 44	297 ± 47	228 ± 47	212 ± 22
	g m^{-2}	4.0 ± 0.7	7.3 ± 1.6	11.5 ± 2.1	8.0 ± 2.2	7.8 ± 0.9
C. caeruleocinctus	Ind. m^{-2}	50 ± 11	124 ± 88	54 ± 11	38 ± 12	66 ± 22
	g m^{-2}	3.3 ± 1.0	2.2 ± 1.3	3.1 ± 0.8	2.4 ± 0.9	2.7 ± 0.5
P. germanicum	Ind. m^{-2}	352 ± 124	311 ± 118	161 ± 62	247 ± 63	267 ± 47
	g m^{-2}	0.4 ± 0.1	0.7 ± 0.2	0.4 ± 0.2	0.4 ± 0.1	0.5 ± 0.1
O. elegans	Ind. m^{-2}	21 ± 14	16 ± 10	1 ± 1	6 ± 3	11 ± 4
	g m^{-2}	ε	ε	ε	ε	ε
P. lagurus	Ind. m^{-2}	119 ± 37	164 ± 37	42 ± 13	121 ± 30	111 ± 16
Total number of Diplopoda	Ind. m^{-2}	643 ± 132	831 ± 142	556 ± 76	640 ± 86	667 ± 56
Total biomass of Chilognatha	g m^{-2}	7.8 ± 1.2	10.3 ± 2.4	15.0 ± 2.4	10.8 ± 2.5	11.0 ± 1.1

s.u. = sampling units. ε = negligible.

The seasonal population densities of the five main species (stadium I not included) are given in Table 1. For each season, the data from the two years are pooled, as differences between years were generally insignificant. However, *G. marginata* was an exception to this rule: in early summer, early autumn, and winter, the numbers of individuals were higher in 1992 than in 1991 ($p < 0.05$); the biomass, too, was higher in the early summer of 1992 ($p < 0.01$).

There were certain significant seasonal changes in population density (Table 1). The number of *G. marginata* was lower in spring than in early summer ($p < 0.05$) and early autumn ($p < 0.01$); likewise, its biomass was lower in spring than in early autumn ($p < 0.01$ for *t*-test; $p < 0.05$ for U-test). The number of *P. lagurus* was lower in early autumn than in early summer ($p < 0.01$) and winter ($p < 0.05$). In all other species, the seasonal variations in numbers of individuals and in biomass were not significant.

RECRUITMENT PERIODS

In millipedes, the first active stadium depends on the species and, as regards those from Puechabon, it is either stadium I (*P. germanicum; P. lagurus*), stadium II (*G. marginata; O. elegans*), or stadium IV (*C. caeruleocinctus*). However, as stadium I is poorly sampled in Tullgren funnels, stadium II is the first to be considered. The abundance of these stadia indicates the periods of the year when the young of each species contribute to the increased density of the community.

In *G. marginata*, recruitment occurs during warm months at Puechabon. Stadium II (8 tergites; 8 leg pairs) was absent in the spring samples but abundant in the samples from early summer (54 individuals m^{-2}) and early autumn (33 individuals m^{-2}). During the latter season, the young of stadia II and III reached a density of 148 individuals m^{-2} in a total of 297; but their biomass did not exceed 0.3 g m^{-2} in a total of 11.5 g.

In *C. caeruleocinctus*, the smallest individuals collected belonged to stadium IV (3 rows of ocelli), as in eastern France (Sahli, 1969). A batch of 15 individuals was found in one sampling unit from the early summer of 1991, between 2 and 10 cm in depth, which may be indicative of the recruitment period. This was confirmed by the appreciable density of the next stadia (V and VI) in early autumn (16 individuals m^{-2} for a biomass of 0.1 g m^{-2}).

Contrary to what could be assumed on the basis of Table 1, the recruitment of *P. germanicum* does not start in winter, but in summer, as in the Atlantic zone (David and Couret, 1985). Indeed, many brooding females were observed in spring, and stadium I individuals in early summer. Afterwards, stadia II and III were sampled in early autumn, though at a relatively low density (19 individuals m^{-2}; negligible biomass).

Unlike the species above, the life cycle of which extends over several years, *O. elegans* is an annual species at Puechabon (David, in prep.). Like most Craspedosomatida from the temperate zone, it breeds in winter, as shown by the appearance of the first stadium II individuals in January (5 individuals m^{-2}), growing rapidly up to stadium V in spring (21 individuals m^{-2}).

P. lagurus is a special case. This species has a short generation time and is probably polyvoltine (Schömann, 1956). Stadia I and II were collected in all seasons, but the samples were not frequent enough to follow this fast-developing species.

VERTICAL DISTRIBUTION

The seasonal changes in the vertical distribution of species between (i) litter and topsoil, and (ii) mineral soil down to 10 cm, are given in Fig. 2 for individual numbers of

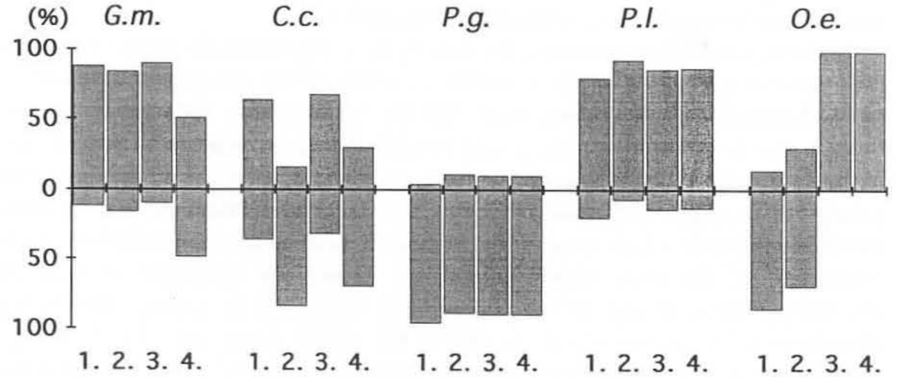

Fig. 2. Changes in the vertical distribution of the principal millipede species (*G.m.*: *Glomeris marginata; C.c.:Cylindroiulus caeruleocinctus; P.g.: Polyzonium germanicum; P.l.: Polyxenus lagurus;* and *O.e.: Opisthocheiron elegans*) in the four seasons (1: spring; 2: early summer; 3: early autumn; 4: winter). The results are expressed as percentages of the number of individuals in two soil layers: (i) litter and topsoil down to 2 cm (above the line); (ii) soil between 2 and 10 cm in depth (under the line).

animals. For the biomass data, not shown in Fig. 2, the results would be the same. The five most abundant species all exhibit different patterns.

G. marginata generally lives near the surface, except in winter when it tends to go deeper. The distribution is the same as in Great Britain, on the opposite side of its range (Bocock and Heath, 1967) — unless there is burrowing at Puechabon in the height of summer, when no samples were taken.

C. caeruleocinctus appears to live a little deeper than *G. marginata* in spring and autumn but, like many iulids in the temperate zone, burrows markedly in summer and winter.

P. germanicum is the most subterranean species at Puechabon. It was always much more abundant in the mineral soil than in the litter and topsoil.

In contrast, *P. lagurus* appears to remain in the litter and upper soil layer throughout the year — also subject to further examination in the height of summer.

As regards *O. elegans*, its population density is low and the proportions given in Fig. 2 are quite uncertain. Nevertheless, the species appears to live in the soil in spring and early summer, then to move upwards in autumn and winter, the breeding period.

DISCUSSION

The seasonality of the Mediterranean climate has little synchronizing effect on the millipede community studied. For example, *G. marginata* burrows in winter and breeds in summer, whereas *O. elegans* burrows in summer and reproduces near the surface in winter. Similarly, in more arid environments, species-specific patterns of life history have been underscored in spirostreptids (Crawford et al., 1987). Seasonal changes in abundance at the millipede community level merely reflect the dynamics of the most abundant species, which change from one ecosystem to another and from one biogeographical zone to another. Therefore, a particular Mediterranean pattern is not expected to be found in the millipede communities.

In the holm oak forest studied, the density of *G. marginata* fluctuates significantly in the course of the year. This species seems to withstand the summer drought easily, since its abundance increases continuously from spring to autumn. The increase in number is largely due to recruitment, the young corresponding on average to 50% of the total number in early autumn. But the increase in biomass results from another cause, the young constituting a very small proportion (3%) of the total biomass in early autumn. A possible explanation is an increase in the fresh body mass of older individuals during the warm half of the year, which amounts to 75 mg per individual in early autumn (excluding stadia II and III) vs. 40 mg per individual in spring. The decrease in abundance of *G. marginata* at the end of the winter is probably due to the species' difficulty in coping with winter cold, as shown by Haacker's (1968) experiments; its tendency to burrow in this season remains limited and mortality can be high.

The abundance of *C. caeruleocinctus* is difficult to assess in summer and winter, when a part of the population probably lives below 10 cm. But the figures for autumn and spring, when it is nearer to the surface, show that its density is stable, in contrast to

G. marginata. This implies that the winter mortality of the iulid must be low and that the recruitment in early summer must also be low or, alternatively, rapidly counterbalanced by high summer mortality. The latter would explain why *C. caeruleocinctus*, in the Montpellier region, is near the warmest and driest boundary of its geographical range (Mauriès, 1964).

The data on *P. germanicum* could not be included in a community dynamics study because the sampling techniques were unsuitable for this deep-soil dweller. As the population density was always much higher in the mineral soil (between 2 and 10 cm deep) than at the surface, it is possible that *P. germanicum* burrows below 10 cm — thus making it difficult to detect seasonal changes in abundance. One would have expected to find the lowest number of individuals just before recruitment, in early summer, which was not the case (see Table 1).

At the community level, the biomass of the two dominant species, *G. marginata* and *C. caeruleocinctus*, fluctuates significantly between a spring minimum of 7.3 ± 1.2 g m^{-2} and an autumn maximum of 14.6 ± 2.3 g m^{-2}. The community is relatively unaffected by the Mediterranean drought owing to the high abundance of *G. marginata*. However, if the minute *P. lagurus* is taken into account, the summer drought has a very negative effect on the number of individuals (see Table 1). The high abundance of *G. marginata* is also largely responsible for the lower spring density. *O. elegans*, owing to its different life cycle, could balance the low number of individuals at the end of the winter, but its peak density is unlikely to greatly influence the community at Puechabon.

G. marginata and *C. caeruleocinctus* are macrosaprophages which chew on litter (Dunger, 1963; Van der Drift, 1975), unlike *P. germanicum* (liquid feeder — Couret, 1985), *P. lagurus* (microphyte grazer — Schömann, 1956) and perhaps *O. elegans* (the staple diet of which is unknown). It is interesting to compare the abundance of macrosaprophagous millipedes (Glomerida, Iulida, and Polydesmida) in forests of different climatic regions of Europe. In the Atlantic zone, the density of these species is very variable, but peak biomasses are usually below 4 g m^{-2}. The highest figures of fresh biomass recorded in Great Britain and northern France are, respectively, 3.9 g m^{-2} in autumn samples from a mixed mull-like moder (Blower, 1979), and 2.3 g m^{-2} in spring and autumn samples from an oak mull (David, 1989). The figure of 7.5 g m^{-2} in a Danish beech mull provided by Bornebusch (1930) may be overestimated, owing to the approximate value of individual biomasses. Similarly, the highest biomass figure recorded in the more continental regions of western Europe is an annual mean of 4 g m^{-2} for all Diplopoda in a mixed oak wood in Austria (Meyer et al., 1984).

Although data are more scarce in European regions of the Mediterranean, they are also very variable from one community to another. Nevertheless, peak biomasses are higher than in the Atlantic zone, notably in climatic transition areas. Iatrou and Stamou (1989) have measured a density of 114 individuals m^{-2} for macrosaprophagous millipedes in a community of northern Greece where *Glomeris balcanica* is dominant, which should correspond to a substantial biomass — above 7.1 g m^{-2}, the figure provided by Iatrou (1989) for *G. balcanica* alone. The macrosaprophage biomass at Puechabon is higher than all those mentioned above, on average 10.5 g m^{-2} for Glomerida and Iulida.

The extent to which these millipedes affect the forest floor depends on their seasonal rate of ingestion of litter, combined with the seasonal changes in biomass measured above. However, if the ingestion rate is of the same order of magnitude as in the conditions prevailing in the Atlantic zone — about 10 g dry litter g^{-1} live weight yr^{-1} for both a glomerid (Van der Drift,1975) and an iulid (David, 1987) — millipedes probably play a very important role in Mediterranean forest ecosystems. At Puechabon, it is possible that they consume over 100 g dry litter m^{-2} yr^{-1}, which would have considerable effects on the decomposition process and the characteristics of the humus. In fact, Bertrand et al. (1987) and Janati-Idrissi (1988) have measured a much lower rate of ingestion by *G. marginata* in Mediterranean conditions (about 3 g dry litter g^{-1} live weight yr^{-1}); but, as they used freshly-fallen leaves which were later proved to be not very edible, this rate should be reassessed using leaves of all ages, closer to the natural diet of millipedes in holm oak forests.

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